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PALEOECOLOGY OF SUBARCTIC FAUNAL ASSEMBLAGES FROM THE WOODFORDIAN AGE (PLEISTOCENE: WISCONSINAN) ELKADER SITE, NORTHEASTERN IOWA

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ABSTRACT Colluvial, fluvial, and alluvial fan sediments at Elkader, Clayton Co., Iowa, contain one of the most tundra-like biotas known from the Pleistocene of midcontinental North America. Remains of animals recovered from the site include open-ground, arctic/subarctic molluscs, beetles (including *Diacheila polita* and *Pterostichus ventricosus*), and mammals (including *Spermophilus parryii, Dicrostonyx torquatus,* and *Microtus* cf. *miurus*). Spruce wood from the fossiliferous horizon yielded a radiocarbon age of 20,530 ± 130 yr B.P. (BETA-2748). Analogs to the insect and mammal faunas from Elkader occur today in subarctic parklands near treeline in northwestern North America. We interpret these assemblages as indicating a subarctic, full-glacial environment at Elkader. Although generally indicative of a cold climate, the molluscan assemblage is more complex in that it includes possible deciduous forest species. This suggests the occurrence of topographically controlled variation in microhabitats at the site. Together, the Elkader assemblages indicate that full-glacial climatic conditions already were well established in northeastern Iowa by 20,500 yr B.P. They confirm the interpretations based on pollen spectra from other Midwestern sites of a tundra-like vegetation and environment in the Upper Mississippi Valley region at this time.

Key words: Beetle; Climate; Coleoptera; Insect; Iowa; Mammal; Mollusc; Paleoecology; Wisconsinan; Woodfordian.

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The environment of the Upper Mississippi Valley region is well documented for some portions of the Wisconsinan glacial stage. Studies of pollen spectra from this region suggest a gradual cooling of the climate from the late Altonian through middle Woodfordian time, although early on the effects of climatic deterioration on the biota may have been limited to more northern parts of the region (Whittecar and Davis, 1982; Baker et al., 1989a,b). During the Farmdalian interstade, about 28,000–25,000 yr B.P., a closed spruce-pine forest covered central and northern Illinois (King, 1979; Whittecar and Davis, 1982; Baker et al., 1989a,b) and eastern Iowa (Mundt and Baker, 1979; Van Zant et al., 1980; Hallberg et al., 1980). Perhaps as early as 26,600 yr B.P., a noticeable shift began to spruce-dominated boreal forest in west-central Illinois (Baker et al., 1989b); this vegetation was well established by ca. 25,000 yr B.P., when Woodfordian ice of the Lake Michigan Lobe began to advance into Illinois (Curry, 1990). After about 22,700 yr B.P. (Baker et al., 1989a,b), or somewhat later (Garry et al., 1990), tundra-like conditions prevailed in northern and central Illinois. The transition into full-glacial conditions by 21,400 yr B.P. is well represented in a mixed boreal forest/tundra insect and plant assemblage at Wedron, LaSalle Co., Illinois (Garry et al., 1990). Tundra-like conditions also were present in east-central Iowa from at least approximately 18,100–17,200 yr B.P. (Baker et al., 1986). After about 17,200 yr B.P., and at least until 16,700 yr B.P., there was a gradual warming trend, and boreal forest or even mixed forest might have been present in east-central Iowa (Baker et al., 1989b). In central Minnesota, tundra-like vegetation is thought to have persisted from at least 20,500–14,700 yr B.P. (Birks, 1976).

Interpretations based on pollen spectra are supported at a few sites by plant macrofossils and fossil beetles. However, few dated Wisconsinan faunal sites containing mammalian fossils are known from the Upper Mississippi Valley region. Conklin Quarry, Johnson Co., Iowa, yielded diverse remains of molluscs, insects, and small mammals, as well as plant macrofossils and pollen, preserved in a swale that filled between about 18,100 and 16,700 yr B.P. (Baker et al., 1986). Moscow Fissure, Iowa Co., Wisconsin, provided a mammalian fauna from approximately 17,000 yr B.P. (Foley, 1984). The Prairieburg site, Linn Co., Iowa, preserved a fauna with a full-glacial aspect, but unfortunately lacks a radiocarbon date (Foley and Raue, 1987). Together, these sites provided preliminary insight into the terrestrial fauna of the Upper Midwest during Woodfordian time.

Fossiliferous terrace deposits at Elkader, Clayton Co., Iowa, provide the oldest and most northern, dated Wisconsinan fauna from the Upper Mississippi Valley region. They offer a rare opportunity to study molluscs, insects, and small mammals that inhabited the full-glacial environment of northeastern Iowa about 20,500 yr B.P.

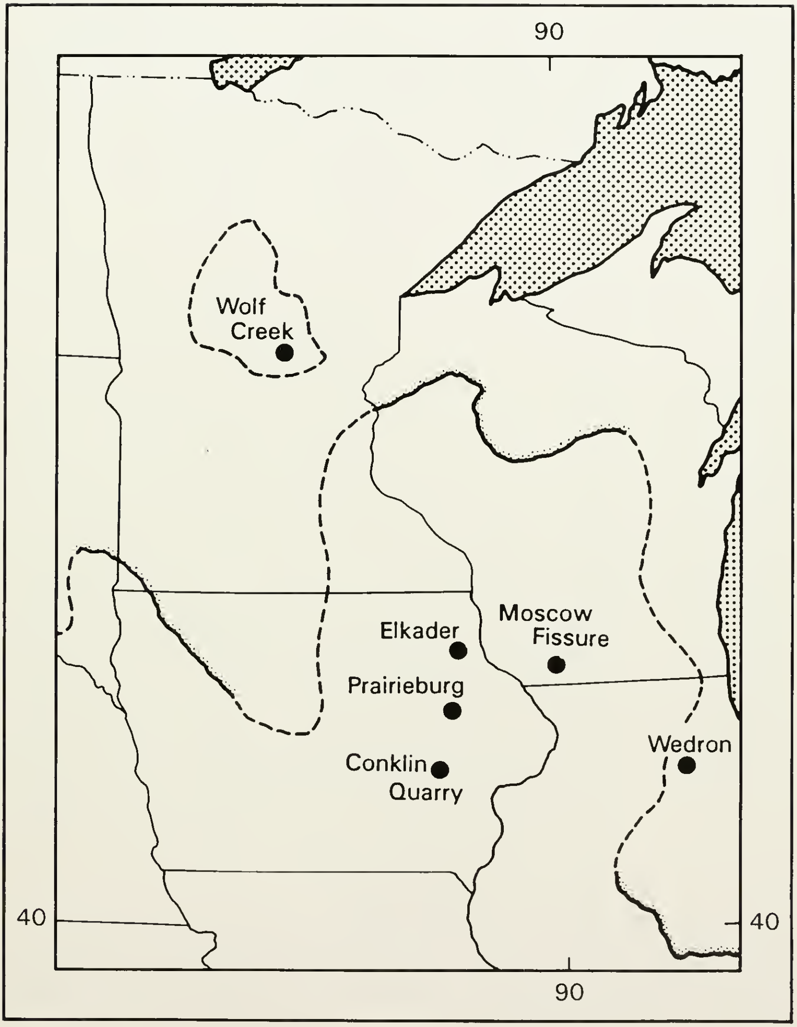


Fig. 1. Location of Elkader and other selected Wisconsinan sites in the Upper Mississippi Valley region. The shaded and dashed lines represent the approximate position of the Laurentide ice front in the region about 20,000–20,500 yr B.P. (after Fenton et al., 1983; Mickelson et al., 1983; Prest, 1984).

SITE DESCRIPTION AND STRATIGRAPHY

The Elkader site is within the incorporated limits of the town of Elkader, Clayton Co., Iowa (SE 1/4, SW 1/4, NE 1/4, Section 23, T. 93 N., R. 5 W.; 42°52"13' N, 91°23"42' W; Fig. 1). The region is one of comparatively high

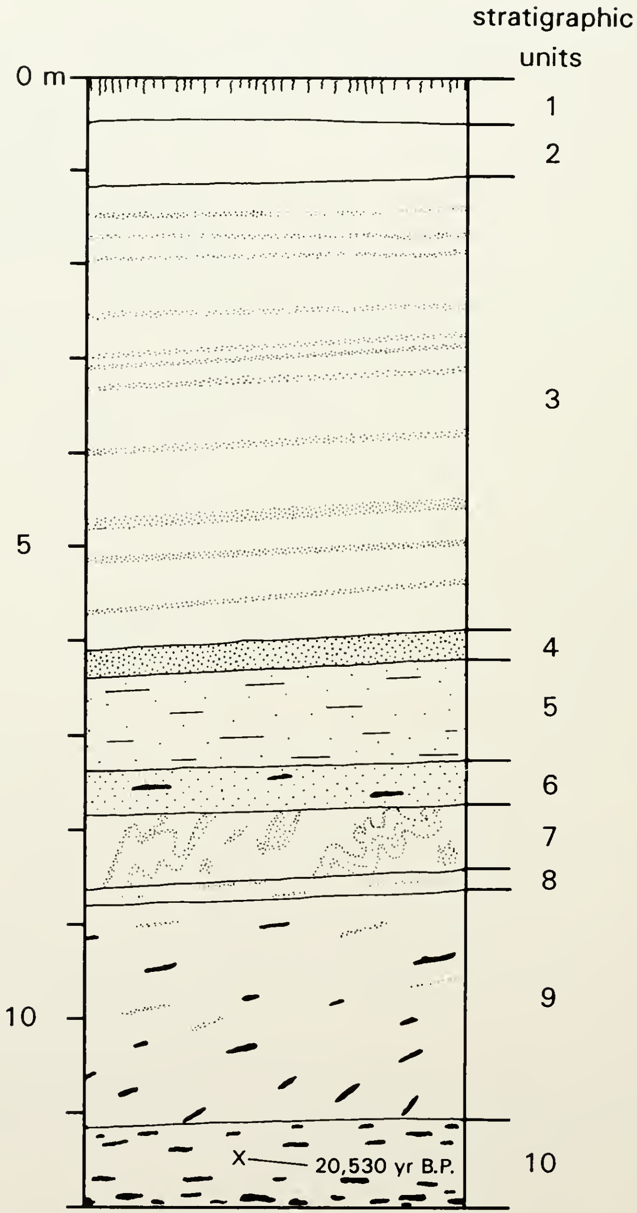


Fig. 2. Composite stratigraphy of the west gulley section at Elkader that was sampled for molluscs (Units 6, 7, 9, 10), insects (Unit 10), and vertebrates (Units 9, 10). Spruce wood, radiocarbon-dated at 20,530 ± 130 yr B.P., was recovered from Unit 10. Descriptions of the stratigraphic units are provided in the text.

relief that was last glaciated in pre-Illinoian time (Hallberg et al., 1984). The site is located in a south-trending gully entrenched into high terrace deposits along the east valley wall of the Turkey River. Fossiliferous sediments were collected primarily from the west side of the gully about midway along its length, where 12 m of colluvium and alluvial fan sediments capped by loess or loess-derived colluvium were exposed (Fig. 2). Complete descriptions of stratigraphic sections were presented by Woodman (1982).

The basal 3.5 m of the section (Units 9 and 10) consist of dark gray, cobble-rich, silt-dominated colluvium. The silt matrix here and in overlying, silt-dominated units probably is reworked loess. The last episode of loess deposition in northeastern Iowa was continuous from about 25,300–14,000 yr B.P. (Ruhe, 1969); contemporaneous erosion and redeposition of loess-derived sediments is thought to have been rapid, owing in part to the high topographic relief in the area (Leigh and Knox, 1994). Spruce wood (*Picea* sp.; F. King, in litt.), recovered from approximately 0.5 m above the base of the section (Unit 10), was dated at 20,530 ± 130 yr B.P. (BETA-2748). Overlying the basal units are about 1.5 m of sediments (Units 6–8) transitional between the colluvial deposits below and alluvial fan deposits upsection. Convolutions up to 0.5 m high in this part of the section (Unit 7) might have resulted from cryoturbation. Interbedded silts and sands in the overlying 6 m of section (Units 3–5) indicate both a fluvial regime and alluvial fan deposition. Southward, toward the terrace escarpment, the deposit grades into fluvial sands and gravels. The section is capped by up to 2.3 m of loess and/or silt-rich colluvium (Units 1 and 2), reworked from upslope loess deposits.

METHODS

Sediments were sampled separately for molluscs, insects, and vertebrates because of the different techniques involved in recovering specimens. Except as noted below, all samples came from the same section.

Because of their abundance and wide distribution at the site, molluscs were collected from a number of different units and at one additional site nearby. Colluvial sediments were sampled in Units 10 (sample MS3; ca. 30 kg) and 9 (MS2; ca. 20 kg). Smaller samples of local alluvium were collected from Unit 6 (MS4; ca. 15 kg) and a 3-cm, probably fluvial, sand at the base of Unit 7 (MS5; ca. 5 kg). Fluvial sand and gravel lag from a small lens (MS6; ca. 2 kg) downslope contained the richest concentration of molluscs of any of the Elkader units. A 25-kg sample of upland loess was bulk-quarried from a 1-m interval above the basal loess paleosol (MS1). Because the predominantly south-facing exposure here was unusual for fossiliferous loess sites, a 15-kg sample was collected from a nearby east and north-facing, calcareous, upland basal loess section (Elkader North: center, NW 1/4, SW 1/4, Sec. 15, R. 5 W., T. 93 N.). Age of the basal loess at Elkader and Elkader North should be comparable. All samples were wet-sieved through a standard series (to 425 μm).

Insect analyses were based on 102 kg of sediment sampled from Unit 10. Because stratigraphic sampling of this unit was inhibited by the presence of large, angular clasts and by the disrupted layering of the colluvium, efforts were concentrated on sampling the thin, organic, laminated silt lenses in the unit instead. Beetles and other insect remains were recovered and prepared for identification using standard procedures (Elias, 1994).

Nearly 4000 kg of matrix were bulk-quarried for vertebrate remains along a 2-m vertical section from approximately 120 cm below the top of Unit 9 to the base of the section. An additional 450 kg of matrix were collected from mottled, olive-gray silts on the gully's east side that correlate with Unit 8 in the west section (Woodman, 1982). All sediments were water-screened on 1.6-mm screen and the residues picked for vertebrate remains.

Specimens are reposited in the collections of the Quaternary Entomology Laboratory, North Dakota State University (insects); and the Repository, Department of Geology, The University of Iowa (molluscs and mammals).

PALEONTOLOGY

We consider the fossils collected from the Elkader site to be entirely autochthonous. The site is located in a small tributary basin approximately a township section (2.59 km^2) in size. Some specimens show wear that may be the result of transport, but the upland borders of the drainage basin are less than 650 m distant horizontally; it is unlikely that animal remains were moved fluvially or colluvially farther than this distance, and there is no evidence of transport by predators. In addition, many of the invertebrate species concur ecologically with the depositional environments interpreted for the sediments in which they occur.

MOLLUSCA

A complete list of the molluscs recovered from Elkader is presented in Table 1. Sample sizes for all units, with the possible exception of Elkader North, likely are large enough to approximate original diversities (Tables 1 and 2). Preservation at Elkader generally is good, and it is noticeably better in alluvial and colluvial samples, in which full ontogenies are present for abundant taxa. Specimens from fluvial samples are somewhat eroded. Provincial affinities, ecology, and modern distributions of molluscan spe-

Table 1. Numbers of specimens of Mollusca from Elkader and vicinity. Figures in parentheses are percentages. Symbols: — = species absent; * = less than 0.5%.

		Elkader					
Taxon	Elkader North	MS1 Loess	MS2 Unit 9	MS3 Unit 10	MS4 Unit 6	MS5 Unit 7	MS6 Sand lens
TERRESTRIAL GASTROPODA:							
Helicinidae							
Hendersonia occulta (Say)	1.0 (*)	—	1.0 (*)	12.0 (1.5)	1.0 (*)	190.0 (13.2)	5.0 (*)
Vallonidae							
Vallonia gracilicosta Reinhardt	5.0 (3.0)	—	—	—	—	—	—
Pupillidae							
Pupilla muscorum Linne	12.0 (7.2)	116.0 (17.3)	52.0 (8.6)	69.0 (8.4)	85.0 (5.1)	51.0 (3.5)	26.0 (3.2)
Vertigo alpestris oughtoni Pilsbry	—	—	2.0 (*)	21.0 (2.6)	5.0 (*)	104.0 (7.2)	16.0 (1.9)
V. hannai (Pilsbry)	—	—	36.0 (5.9)	121.0 (14.8)	1.0 (*)	2.0 (*)	12.0 (1.5)
V. modesta modesta (Say)	16.0 (9.6)	19.0 (2.8)	111.0 (18.3)	135.0 (16.5)	169.0 (10.2)	44.0 (3.0)	79.0 (9.6)

Table 1. Continued.

Taxon	Elkader North	Elkader					
		MS1 Loess	MS2 Unit 9	MS3 Unit 10	MS4 Unit 6	MS5 Unit 7	MS6 Sand lens
V. modesta parietalis (Ancey)	—	—	22.0	27.0	34.0	7.0	11.0
			(3.6)	(3.3)	(2.1)	(*)	(1.3)
V. occulta Leonard	—	—	—	1.0	1.0	—	1.0
				(*)	(*)		(*)
Columella alticola (Ingersoll)	10.0	—	156.0	86.0	482.0	383.0	209.0
	(6.0)		(25.7)	(10.5)	(29.2)	(26.5)	(25.4)
Succineidae							
Catinella gelida (Baker)	33.0	312.0	173.0	224.0	283.0	262.0	221.0
	(19.8)	(46.5)	(28.5)	(27.3)	(17.1)	(18.1)	(26.9)
Succinea bakeri Hubricht	1.0	207.0	—	—	—	5.0	75.0
	(*)	(30.8)				(*)	(9.1)
Discidae							
Discus whitneyi (Newcomb)	—	—	—	—	—	—	13.0
							(1.6)
D. macclintocki (Baker)	—	—	—	3.0	—	1.0	2.0
				(*)		(*)	(*)
D. shimeki (Pilsbry)	88.0	—	46.0	111.0	590.0	237.0	94.0
	(52.7)		(7.6)	(13.5)	(35.7)	(16.4)	(11.4)

Table 1. Continued.

		Elkader					
Taxon	Elkader North	MS1 Loess	MS2 Unit 9	MS3 Unit 10	MS4 Unit 6	MS5 Unit 7	MS6 Sand lens
Helicodiscidae							
Helicodiscus parallelus (Say)	—	—	—	1.0 (*)	—	—	—
Limacidae							
Deroceras laeve Müller	1.0 (*)	17.0 (2.5)	7.0 (1.2)	9.0 (1.1)	—	21.0 (1.5)	9.0 (1.1)
Zonitidae							
Euconulus fulvus (Müller)	—	—	—	—	—	2.0 (*)	—
AMPHIBIOUS GASTROPODA:							
Lymnaeidae							
Fossaria (Bakerlymnaea) dalli (Baker)	—	—	—	—	—	4.0 (*)	5.0 (0.6)
F. (Fossaria) exigua (Lea)	—	—	—	—	—	118.0 (8.2)	39.0 (4.7)
F. (Fossaria) parva (Lea)	—	—	—	—	—	13.0 (0.9)	5.0 (0.5)
TOTAL NUMBER OF SPECIMENS	167.0	671.0	606.0	820.0	1651.0	1444.0	822.0
TOTAL NUMBER OF SPECIES	9	5	10	13	10	16	17

Table 2. Distribution and occurrence of land snails at Elkader and Conklin Quarry. Abbreviations and symbols: **E** = extinct; I = Interior Province; MW = Midwest Biome or other Pleistocene assemblage; N = Northern Province; **R** = relict distribution, not assigned to a modern province; RM = Rocky Mountain Province, western division; + = present; — = absent.

	Modern distribution		Fossil distribution							
					Elkader					
Taxon	Molluscan faunal province	Occurrence in Iowa	Conklin Quarry	Elkader North	MS1	MS2	MS3	MS4	MS5	MS6
Terrestrial Gastropoda:										
Helicinidae										
Hendersonia occulta (Say)	MW(R)	**R**	+	+	—	+	+	+	+	+
Vallonidae										
Vallonia gracilicosta Reinhardt	RM	**R**	+	+	—	—	—	—	—	—
Cionellidae										
Cochlicopa lubrica (Müller)	C	+	+	—	—	—	—	—	—	—
Pupillidae										
Pupilla muscorum muscorum Linne	N	—	+	+	+	+	+	+	+	+
Vertigo alpestris oughtoni Pilsbry	N	—	+	—	—	+	+	+	+	+
V. elatior Sterki	N	**R**	+	—	—	—	—	—	—	—
V. hannai (Pilsbry)	MW(**E**)	—	+	—	—	+	+	+	+	+
V. modesta modesta (Say)	N	—	+	+	+	+	+	+	+	+
V. modesta parietalis (Ancey)	N	—	—	—	—	+	+	+	+	+
V. occulta Leonard	MW(**R**)	**R**	—	—	—	—	+	+	—	+
Columella alticola (Ingersoll)	RM	**R**?	+	+	—	+	+	+	+	+

Table 2. Continued.

	Modern distribution		Fossil distribution							
					Elkader					
Taxon	Molluscan faunal province	Occurrence in Iowa	Conklin Quarry	Elkader North	MS1	MS2	MS3	MS4	MS5	MS6
Succineidae										
Catinella gelida (Baker)	MW(**R**)	**R**	+	+	+	+	+	+	+	+
Succinea bakeri Hubricht	MW(E)	—	+	+	+	—	—	—	+	+
S. pleistocenica (Baker)	MW(E)	—	+	—	—	—	—	—	—	—
Discidae										
Discus whitneyi (Newcomb)	C	+	+	—	—	—	—	—	—	+
D. macclintocki (Baker)	MW(**R**)	**R**	—	—	—	—	+	—	+	+
D. shimeki (Pilsbry)	RM	—	+	+	—	+	+	+	+	+
Helicodiscidae										
Helicodiscus parallelus (Say)	C	+	—	—	—	—	+	—	—	—
Limacidae										
Deroceras laeve Müller	C	+	+	+	+	+	+	—	+	+
Zonitidae										
Euconulus fulvus (Müller)	C	+	+	—	—	—	—	—	+	—
Polygyridae										
Webbhelix multilineata (Say)	I	+	+	—	—	—	—	—	—	—
Oreohelicidae										
Oreohelix strigosa iowensis (Pilsbry)	RM	—	+	—	—	—	—	—	—	—
TOTAL NUMBER OF SPECIES			18	9	5	10	13	10	13	14

cies recovered from Elkader were provided by Frest and Dickson (1986). Modern distributions are based on Pilsbry (1939–1948) and Hubricht (1985). Wisconsinan distributions are based on various sources. Unusual taxa are discussed below.

Vertigo hannai

This extinct pupillid has an Illinoian-to-Wisconsinan geological distribution. It has been reported from a few Woodfordian sites in Kansas, Iowa, Illinois, and Indiana (Baker et al., 1986:fig. 3). In western Iowa, the species occurs only in sites transitional between the Pleistocene Midwest and Taiga Biomes of Frest and Fay (1980; also Frest and Dickson, 1986:140). The Taiga Biome is hypothesized to have been an irregular band of boreal, coniferous forest with some open parkland that extended from Kansas through Ohio. The Midwest Biome is based on a widespread nonanalogous fauna (sensu Semken, 1988) of molluscs that is typified by a number of endemic species. The biome is believed to have occurred south of the Taiga Biome in northern Missouri, parts of central and southern Illinois, and southern Indiana. The vegetation associated with the Midwest Biome is interpreted to have included a few tree species from both the taiga and mixed coniferous forest-deciduous forest, and the environment is thought to resemble the modern ecotone between those two biomes. Frest and Fay (1980) hypothesized that a more equable climate, with reduced temperature extremes and more available moisture than at present, permitted the coexistence of Midwest Biome species.

Vertigo occulta

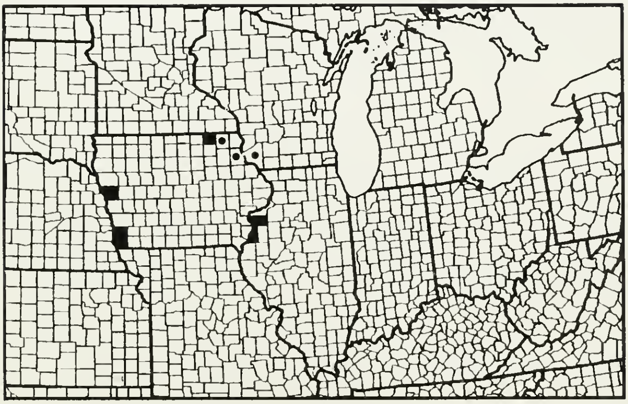
This species is typical of the Midwest Biome and has a pre-Illinoian-to-Wisconsinan fossil range. Currently, *Vertigo occulta* is a relict species known from six sites in the Paleozoic Plateau in Iowa and Wisconsin. It has been recovered from a few Woodfordian sites in Iowa and western Illinois. Reexamination of specimens identified as *V. occulta* from other fossil sites indicates that some are large *Vertigo nylanderi* Sterki, a related species. Only records confirmed by T. Frest are plotted in Figure 3.

Vertigo modesta parietalis

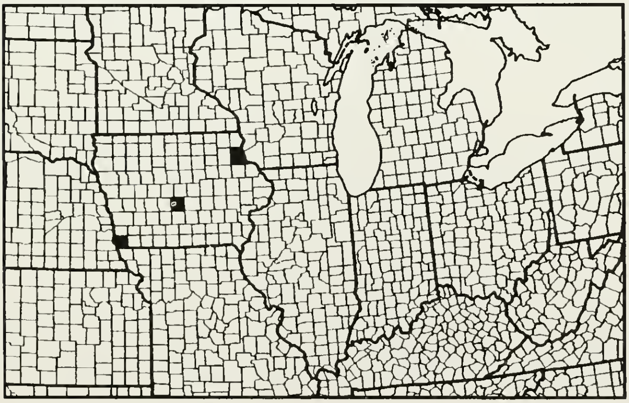
This taxon has a limited modern distribution within the range of *Vertigo modesta modesta* (Say) in the Northern Province in Canada (Pilsbry, 1948). There is only one previous record from Peoria Loess (Woodfordian) in western Iowa (Frest and Dickson, 1986). Examination of large numbers of Woodfordian specimens of the *V. modesta* complex from Iowa, Illinois, and Nebraska yielded additional *V. m. parietalis* (Fig. 3), all from sites in the Taiga Biome.

Fig. 3 (opposite). Distributions by county of selected Elkader molluscs. Dots indicate living (relict) records; filled counties are late Wisconsinan (Woodfordian) sites.

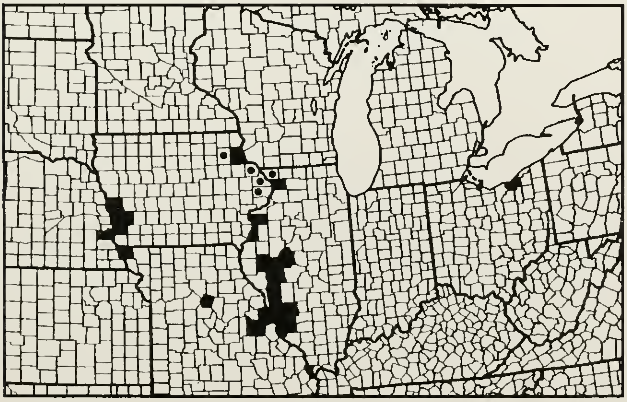
Vertigo occulta



Vertigo modesta parietalis



Discus macclintocki



Succinea pleistocenica

This taxon was reported as *Succinea* sp. at Conklin Quarry (Baker et al., 1986). The Pleistocene fossil record for this extinct species is poorly known, in part because of confusion with *Succinea chittenangoensis* (Pilsbry) and an undescribed relict species from Minnesota and Iowa.

Discus macclintocki

Discus macclintocki also typifies the Midwest Biome. The fossil record of this species ranges from pre-Illinoian to Holocene, and late Woodfordian loess records are known from Nebraska, Iowa, Missouri, Illinois, and Ohio. Twenty-eight small relict colonies are known in the Paleozoic Plateau in Iowa and Illinois (Fig. 3).

Fossaria (Bakerilymnaea) dalli

Today, *Fossaria dalli* is uncommon in Iowa, where it occurs in permanent lakes and ponds, marshes, and small streams. It occupies similar habitats in southern Ontario and the southern Prairie Province in Canada (Clarke, 1981).

Fossaria (Fossaria) exigua

In Canada, this small, aquatic snail inhabits mud substrates "in protected parts of lakes and ponds, in backwater areas of rivers, in swamps, and in subarctic muskeg pools" (Clarke, 1981:100).

Fossaria (Fossaria) parva

This amphibious species is common in eastern Iowa, and is known to occur in marshes, wet mud flats, and near the water's edge on lake shores and river banks south of tree line in Canada (Clarke, 1981).

Discussion.—The interpretations of sedimentological units at Elkader as representing fluvial, alluvial, colluvial, and eolian upland environments based on geomorphic and pedological evidence (Woodman, 1982; Hallberg and Bettis, 1985) are supported by their molluscan faunas. This is especially striking because (with the exception of the upland loess sample [MS1] and the Elkader North site) mollusc samples were collected from within an area no more than 150 m long. The upland and basal slope faunas are distinct, as are the two upland slope exposures.

None of the units has a mollusc assemblage with a modern analog (Tables 2, 3), and no Interior Province endemics (i.e., much of the Elkader area's current land snail fauna) are present. All assemblages have major Rocky Mountain and Northern Province taxa; most include trace Midwest Biome species, and all have significant numbers of extinct taxa.

Table 3. Provincial affinities and diversities of molluscan faunas from Elkader and Conklin Quarry. Figures are numbers of species. Figures in parentheses are percentages. Abbreviations and symbols as in Tables 1 and 2.

	Molluscan faunal province					
Locality	C	RM	N	MW	I	Total no. of species
Loess:						
Conklin Quarry	4 (23.5)	3 (17.6)	3 (17.6)	6 (35.2)	1 (5.8)	17
Elkader North	1 (11.1)	3 (33.3)	2 (22.2)	3 (33.3)	—	9
MS1	1 (20.0)	—	2 (40.0)	2 (40.0)	—	5
Colluvium:						
MS2	1 (10.0)	2 (20.0)	4 (40.0)	3 (30.0)	—	10
MS3	2 (15.4)	2 (15.4)	4 (30.8)	5 (38.5)	—	13
Alluvium:						
MS4	—	2 (20.0)	4 (40.0)	4 (40.0)	—	10
Fluvium:						
MS5	2 (15.4)	2 (15.4)	4 (30.8)	5 (38.5)	—	13
MS6	2 (14.3)	2 (14.3)	4 (28.6)	6 (42.9)	—	14

The Elkader upland loess assemblage (MS1) has an unusually low diversity, perhaps because of the southern exposure of the site. The assemblage from nearby east- and north-facing Elkader North has almost twice the diversity, and the assemblage from the Conklin Quarry site contains more than three times the diversity of the upland loess site (Table 2). Most individuals in the upland loess assemblage are extinct and relict succineids; slugs and small pupillids together account for only about 23% of the fauna (Table 1). The presence of slugs and the abundance of succineids suggests an open, cold, but not intensely xeric, environment. If the interpretation of the Conklin Quarry upland and swale sites as a partly open, tundra-treeline analog is correct (Baker et al., 1986), the upland at Elkader probably was a still more open and tundra-like habitat.

The basal colluvial slope assemblages (MS2, MS3) contrast sharply with that of the upland loess. Diversity is more than double that of the upland sample (Tables 1, 2), and the presence of small numbers of the Midwest Biome species *Hendersonia occulta, Vertigo occulta,* and *Discus macclintocki* is noteworthy. Elkader is the most northerly Wisconsinan site for these taxa. Experiments by Frest indicated that the surviving Midwest Biome taxa are stenothermal, glacially adapted calciphiles. *Vertigo occulta* and *Discus macclintocki* feed almost exclusively on deciduous leaf litter, particularly leaves of birch (*Betula*), but also of maple (*Acer*) and ash (*Fraxinus*). Their presence suggests the limited persistence of stands of deciduous trees in protected lowlands relatively near the Wisconsinan glacial margin.

Slope-base, fluvial deposits (MS5, MS6) have comparatively high diversities, with the additional taxa being mostly aquatic snails of the genus *Fossaria.* These assemblages closely resemble that from Conklin Quarry (Baker et al., 1986), except for the inclusion of Midwest Biome taxa.

The local alluvial assemblage (MS4) has a diversity and species composition comparable to those of the colluvial sites (MS2, MS3).

Collectively, the Elkader molluscs suggest a well-differentiated glacial environment consisting of a mosaic of microhabitats, although it was tundra-like overall. Excluding extinct and relict components, the assemblages are most closely analogous to those of subarctic parkland near the boreal forest-tundra ecotone. However, the limited persistence of taxa that typify the Midwest Biome suggests the local presence of warmer microclimates. The environment at Elkader probably resembled that interpreted for Conklin Quarry, but with colder uplands and a slightly more extensive deciduous component in topographically protected situations.

The results from Elkader contrast with previous interpretations from upland loess showing a more regionally homogeneous pattern of recurrent land-snail assemblages within more or less consistent biomes (Leonard and Frye, 1960; Frest and Fay, 1980). The Elkader molluscs more closely resemble a situation hypothesized by Rhodes (1984) to explain non-analogous assemblages of small vertebrates associated with alluvial fills in the Loess Hills of western Iowa.

INSECTS

Insect remains at Elkader are sparse relative to those of other late Wisconsinan sites, and most are worn and fragmented. A complete list of the taxa identified from Elkader is provided in Table 4. Beetles dominate the assemblage, and ground beetles (Carabidae) are particularly well repre-

Table 4. Coleoptera and other insect fossils from Elkader. Numbers in parentheses refer to the number of indeterminate species within a taxon. Abbreviations for skeletal parts are: H = head; P = pronotum; L = left elytron; R = right elytron. Minimum numbers of individuals (MNI) are based on the most abundant skeletal part.

Taxon	MNI	Skeletal parts
COLEOPTERA:		
Carabidae:		
Notiophilus cf. *borealis* Harris	2	HPLR
Diacheila polita Fald.	1	R
Dyschirius melancholichus Motsch.	4	PLR
Miscodera arctica (Payk.)	3	PR
Bembidion cf. *morulum* LeC.	1	P
Bembidion spp.	3	HPLR
Pterostichus (Cryobius) barryorum Ball	2	PLR
Pterostichus (Cryobius) ventricosus (Eschz.)	3	P
Pterostichus (Cryobius) spp.	7	HPLR
Amara obesa (Say)	3	HPR
Cymindis unicolor Kby.	2	P
Hydrophilidae:		
Helophorus sp.	1	R
Staphylinidae:		
Olophrum rotundicolle (C.R. Sahlb.)	1	PR
Acidota crenata Fab.	2	LR
Stenus spp. (2)	2	LR
Quedius fellmanni (Zett.)	1	H
Mycetoporus sp.	2	PL
Aleocharinae gen, indet.		
Silphidae:		
Thanatophilus trituberculatus (Kby.)	1	PR
Scarabaeidae:		
Aegialia sp.	1	R
Aphodius sp.	1	L
Byrrhidae:		
Curimopsis sp.	3	HLR
cf. *Cytilus* sp.	3	PLR
Heteroceridae:		
Gen. indet.	1	PR
Elateridae:		
Gen. indet.	1	PR

Table 4 Continued.

Taxon	MNI	Skeletal parts
Chrysomelidae:		
cf. *Chrysolina* sp.	2	HPL
Curculionidae:		
Lepyrus sp.	1	LR
Gen. indet.	5	HPLR
HEMIPTERA:		
Saldidae:		
Gen. indet.	2	H
Pentatomidae:		
Gen. indet.	2	H
HOMOPTERA:		
Cicadellidae:		
Gen. indet.	2	H

sented. Remains of aquatic and shoreline insects (e.g., Hydrophilidae, Heteroceridae, Saldidae) are scarce: those few species present are typical of shallow water or water-marginal environments. Bark beetles and other forest or woodland taxa are absent. Without exception, terrestrial insects from the Elkader site are presently open-ground inhabitants; of these, the following four are of particular interest.

Diacheila polita

In northwestern North America, this species occurs on open, peaty soil (Lindroth, 1961) in regions from the Anderson River Delta (Morgan et al., 1982) westward (Fig. 4). In Iowa, fossils of *Diacheila polita* also were recorded from Conklin Quarry (Baker et al., 1986) and from Saylorville at approximately 15,400 yr B.P. (Schwert, 1992). In Illinois, *D. polita* was reported from about 19,700-yr-B.P. sediments at Peoria (Gardena section, Morgan et al., 1982), from about 20,670-yr-B.P. sediments at Clinton (Morgan and Morgan, 1986), and from about 21,500-yr-B.P. sediments at Wedron (Garry et al., 1990). The biogeographical significance of its late Wisconsinan occurrences in the Midwest have been discussed by Schwert and Ashworth (1988) and Schwert (1992).

Pterostichus (Cryobius) ventricosus

This species has a subarctic distribution (Fig. 4) similar to that of *Diacheila polita* (Schwert and Ashworth, 1988). It has been recorded in Iowa from Conklin Quarry (Baker et al., 1986).

Pterostichus (Cryobius) barryorum

According to Lindroth (1966), this beetle is "primarily a tundra species." The relatively few modern records (Fig. 5) indicate a distribution similar to those of both *Diacheila polita* and *Pterostichus ventricosus*, although *Pterostichus barryorum* has been collected as far south as Fort McMurray, Alberta. In Iowa, fossil *P. barryorum* were recovered from Conklin Quarry (Baker et al., 1986).

Amara obesa

This species has a trans-American distribution (Fig. 5). It has been recorded from localities as far south as Arkansas (Lindroth, 1968) and as far north as Alaska, but nowhere does its range approach arctic treeline. However, we (D.P.S. and A.C.A.) collected *Amara obesa* on alpine tundra (elev. 3170 m) in the Beartooth Mountains of Montana, indicating that it is capable of living under subarctic conditions.

Discussion.—*Amara obesa* was the only insect species identified at Elkader that was not recorded also from Conklin Quarry by Baker et al. (1986). None of the open tundra ground beetles (e.g., *Pterostichus vermiculosis, P. sublaevis*) present at Conklin Quarry occurs at Elkader. Except for *A. obesa*, all species identified at Elkader occur today at or near the arctic treeline. The closest analogs to this fauna exist at treeline in Alaska and the northern Yukon, where mean July temperatures range from 12–14°C.

Pterostichus ventricosus and *Diacheila polita* are subarctic beetles that occupied both Beringia (Matthews, 1974; 1975) and the southern margin of Laurentide ice during the late Wisconsinan maximum. Late Wisconsinan climatic warming extirpated populations of these and most other arctic species in the Midwestern United States by about 14,000 yr B.P. (Schwert and Ashworth, 1988; Schwert, 1992), but Beringian populations of these species were not subjected to late glacial extinction. Beringia therefore served as the principal center of origin for the postglacial dispersal of arctic beetles. Eastward dispersal of the flightless species *D. polita* and *P. ventricosus* across the arctic may have been delayed by such geographic obstacles as the maze of distributaries and the northward extension of forest at the Mackenzie River Delta. Hence, unlike more motile species of arctic beetles, their modern ranges are still limited to the northwest (Fig. 4).

MAMMALS

In general, mammal remains from Elkader are scarce, and individuals are represented primarily by teeth; only a few bony elements were recovered. If all mammalian remains from the site are treated as a single,

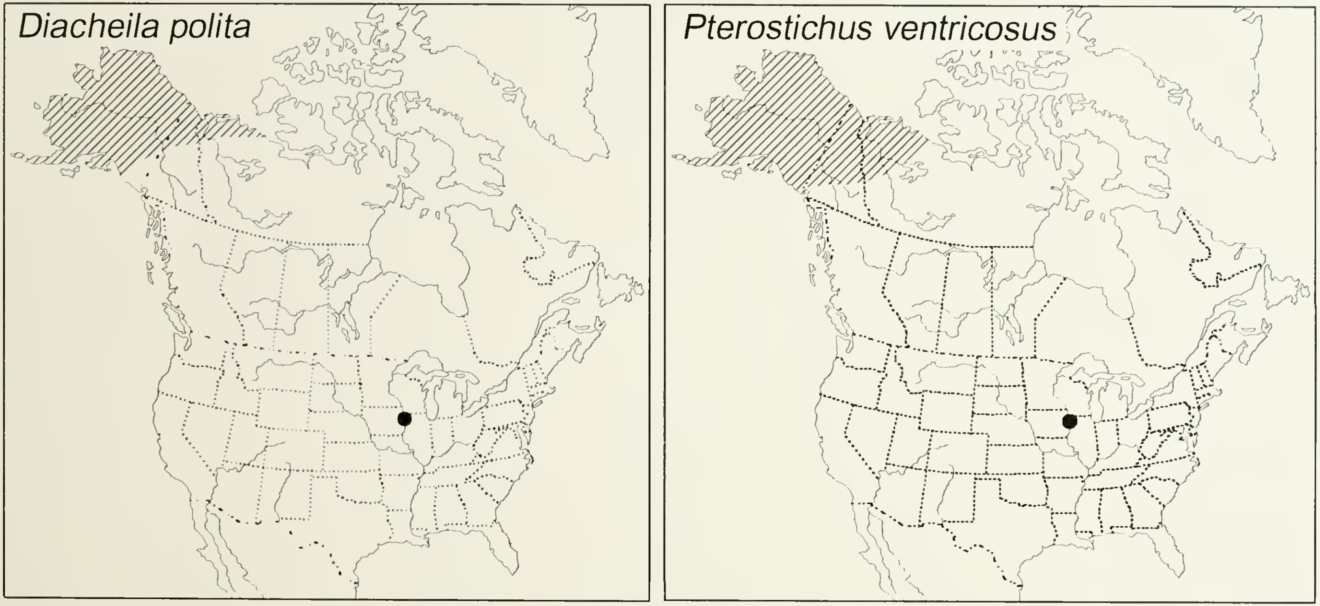


Fig. 4. Modern North American distributions of the carabid beetles *Diacheila polita* and *Pterostichus (Cryobius) ventricosus*.

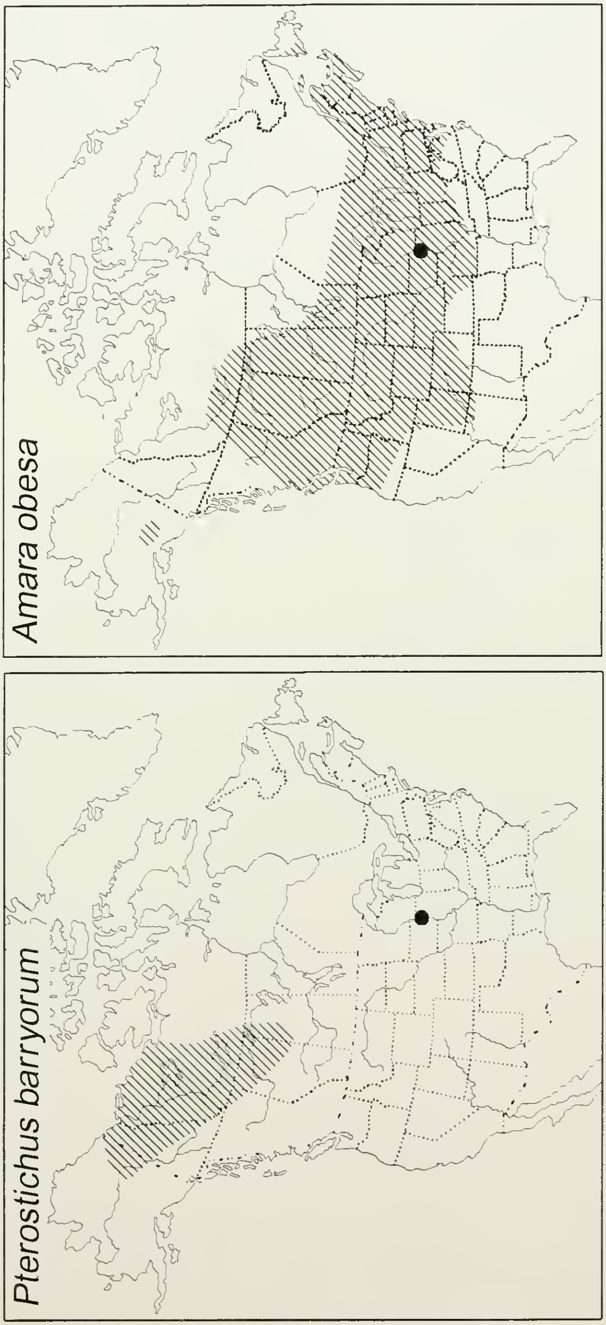


Fig. 5. Modern North American distributions of the carabid beetles *Pterostichus* (*Cryobius*) *barryorum* and *Amara obesa*.

contemporaneous fauna, a minimum of 15 individuals representing six rodent species were identified (Table 5). Three species (*Spermophilus parryii, Dicrostonyx torquatus,* and *Microtus miurus*) are modern inhabitants of the subarctic; two species (*Clethrionomys* sp. and *Microtus xanthognathus*) are typical of boreal, coniferous forests, and one (*Microtus pennsylvanicus*) is cosmopolitan. Ecologies of these mammals were described by Banfield (1974) and Bee and Hall (1956). Modern distributions follow Hall (1981).

Remains of mammals tended to be more concentrated in the basal sediments; all species of mammals recorded from the site were represented in Unit 10 (Table 6). Only *Dicrostonyx torquatus* and *Microtus* cf. *miurus* were recovered from Unit 9, and *Microtus* cf. *miurus* was the only taxon obtained from the east side of the gully. Species of particular interest are described in detail below.

Spermophilus parryii

Modern arctic ground squirrels inhabit open tundra and brushy clearings in coniferous forests of northwestern Canada and Alaska (Fig. 6). Elkader and the undated Prairieburg site (Foley and Raue, 1987) are the only known fossil localities for *Spermophilus parryii* from south of the Laurentide ice sheet.

On the basis of studies of transferrin allele frequencies in modern arctic ground squirrels, Nadler and Hoffmann (1977) concluded that most modern North American and Siberian *Spermophilus parryii* arose from interbreeding Wisconsinan populations inhabiting Beringia. However, one North American subspecies, *S. parryii plesius,* has greater divergences in allele frequencies than those found among the other subspecies of *S. parryii.* On this basis, Nadler and Hoffmann (1977) suggested that it had occupied a separate Wisconsinan refugium. Preliminary comparisons of Elkader specimens with five subspecies of modern *S. parryii* from Alaska and Canada indicated that the fossils are closest in size and morphology to *S. p. plesius* (Woodman, 1982). This supports the hypothesis of a separate refugium for the ancestors of *S. p. plesius* and suggests a refugium south of continental ice. This hypothesis is supported further by modern distributional patterns of fleas (Siphonaptera) of arctic ground squirrels (Holland, 1963). These indicate past contact between one or more southern populations of the arctic ground squirrel (*S. p. ablasus, S. p. kodiacensis, S. p. nebulicolus, S. p. plesius*) and the Columbian ground squirrel (*Spermophilus columbianus*), that today occurs in portions of southern British Columbia, southern Alberta, western Montana, Idaho, eastern Oregon, and eastern Washington.

Dicrostonyx torquatus

The collared lemming is an Holarctic, tundra species with a North American distribution in Alaska and northern Canada west of Hudson Bay.

Table 5. Mammals from the Elkader local fauna: minimum numbers of individuals (MNI) and identified dental remains. Abbreviations and symbols used are: L = left; R = right; m = lower molar; M = upper molar; * = tooth fragment.

Taxon	MNI	Identified elements
Sciuridae		
Spermophilus parryii (Richardson)	1	RP4, LMI
Muridae		
Dicrostonyx torquatus (Pallas)	3	2 Lm1, 2 Lm2, Lm3, 2 RM1, 3 LM1, 3 RM2, 2 LM2, 2 RM3, Lm2/Lm3*
Clethrionomys undif.	1	RM1
Microtus undif.	3	5 Rm1*, Lm1*, 2 Rm2, 3 Lm2, Rm3, 4 RM1, 5 LM1, RM2, RM3, LM3
M. cf. *miurus* Osgood	5	2 Rm1, 5 Lm1, 2 RM2, LM2
M. pennsylvanicus (Ord)	1	Rm1, Lm1, RM2
M. xanthognathus (Leach)	1	LM1
TOTAL NUMBER OF INDIVIDUALS	15	

Table 6. Mammal remains recovered from the Elkader site, by stratigraphical unit. Numbers of identified remains are those elements identified to species. Numbers in parentheses are the percentages represented in each unit.

Stratigraphical unit	Number of identified remains	Total number of remains	Field weights of sediments excavated (kg)
East side	2 (4)	3 (3)	756 kg (19)
Unit 9	8 (15)	15 (15)	1568 kg (40)
Unit 10	45 (81)	84 (82)	1624 kg (41)
TOTALS	55	102	3948 kg

The related Labrador collared lemming, *Dicrostonyx hudsonius,* inhabits tundra east of Hudson Bay. Both North American species are represented in late Pleistocene sites south of the Wisconsinan glacial margin (Fig. 6). The presence of *Dicrostonyx* normally is associated with cold, dry, sparsely vegetated environments (King and Graham, 1986).

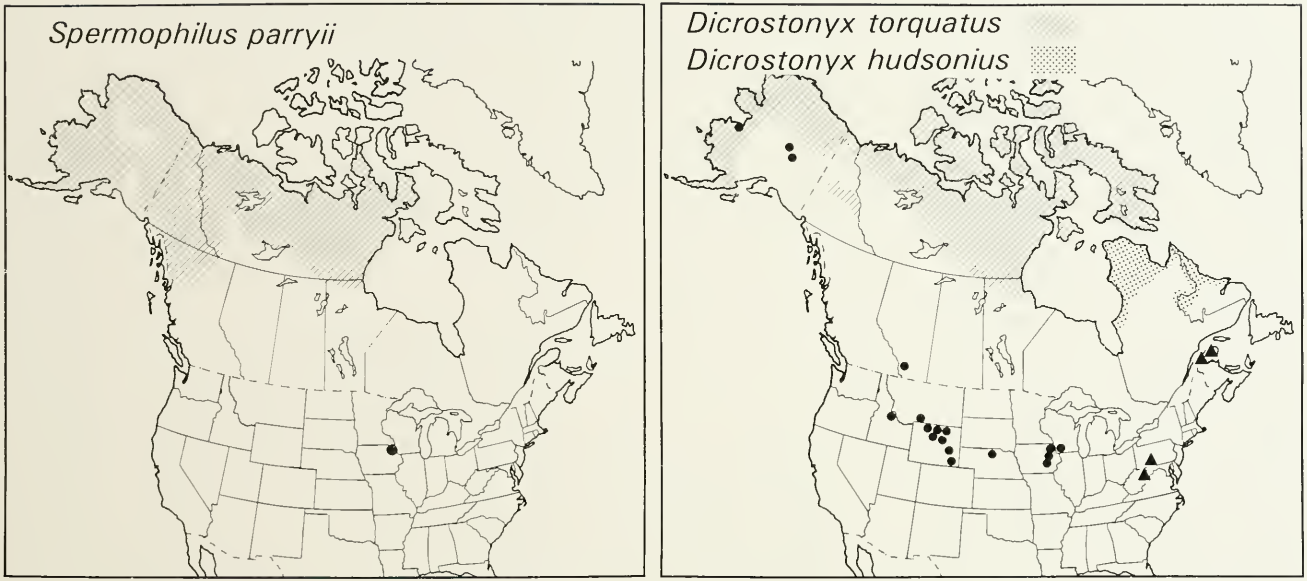


Fig. 6. North American distributions of selected mammals from Elkader: modern distribution of *Spermophilus parryii;* modern (shading) and Wisconsinan (dots) distributions of North American *Dicrostonyx.*

Microtus cf. *miurus*

The singing vole is the most abundant mammal represented in the Elkader fauna. Modern *Microtus miurus* occur in dry arctic and subarctic tundra and on well-drained ground near water in alpine tundra in northwestern Canada and Alaska (Fig. 7).

Dental remains ascribed to this taxon most resemble those of modern *Microtus miurus*, but there are subtle differences. The lower first molars of modern *M. miurus* possess either five or six closed triangles and are characterized by a fourth buccal reentrant that is slightly wider and shallower than that seen in the meadow vole, *M. pennsylvanicus* (Fig. 8). Fossil lower first molars from Elkader fall within the range of variation of *M. miurus*, but there is a tendency for the fourth buccal reentrant to be even shallower (almost nonexistent in some cases). Upper second molars referred to *M. miurus* lack the posterior fifth loop characteristic of *M. pennsylvanicus*, and they are much smaller than those of *M. xanthognathus*. Morphologically similar molars of *Microtus* were recovered from Conklin Quarry (Baker et al., 1986) and Prairieburg (Foley and Raue, 1987).

Microtus xanthognathus

The yellow-cheeked vole is considered to be a representative of a boreal environment (Graham, 1976), and its presence has been interpreted as indicating the presence of taiga (Guilday, 1971) or open spruce-deciduous parkland (Hallberg et al., 1974). Modern *Microtus xanthognathus* is an early-colonizing species that prefers areas with mossy ground cover and requires sources of storagable rhizomes for surviving winter (Wolff and Lidicker, 1980). It has been positively associated with grasses, one of its primary food resources; a similar association with black spruce (*Picea mariana*) (Douglass, 1977) may represent only summer expansions of local territories and food preferences (Wolff and Lidicker, 1980).

This large vole has been recorded from numerous Wisconsinan faunas (Woodman, 1982). In the Upper Mississippi Valley, remains of *Microtus xanthognathus* were reported from Conklin Quarry (Baker et al., 1986), Eagle Point (Rosenberg, 1983), and Moscow Fissure (Foley, 1984).

Discussion.—The low numbers of mammalian species in the Elkader (7 taxa) and Conklin Quarry (8 taxa) assemblages are thought to reflect the low diversities typical of subarctic environments. That the low species richness is not simply an artifact of low numbers of individuals is confirmed by the Prairieburg assemblage (Foley and Raue, 1987); this site yielded abundant mammal remains representing more than 86 individuals, but only eight species of mostly tundra and boreal forest mammals.

The subarctic rodents from Elkader represent one of the few Wisconsinan mammalian assemblages with a modern analog. Elkader also has one of the

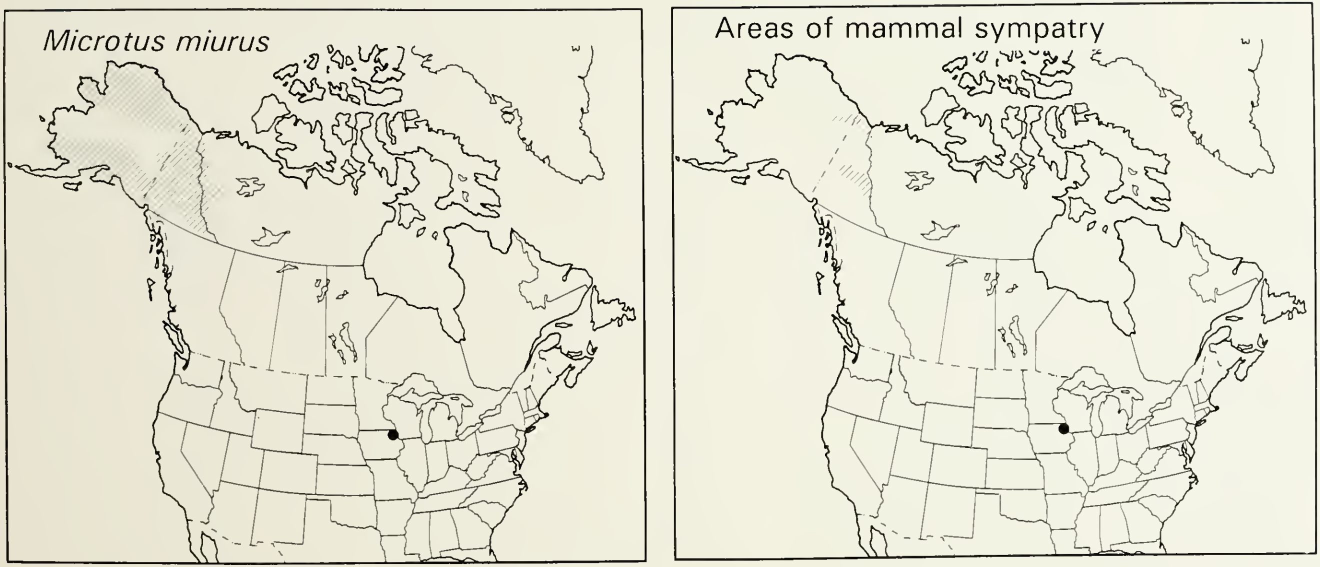


Fig. 7. Modern North American distribution of *Microtus miurus;* and areas of modern sympatry for all mammals from Elkader.

highest concentrations of cold-adapted mammals ever recorded south of the maximum extent of Laurentide ice. The zone of modern sympatry (sensu Semken, 1988), where the modern ranges of all mammalian taxa represented at Elkader overlap, consists of two areas in northwestern North America (Fig. 7). The southern area is within the limits of discontinuous permafrost, and the northern area is in a region of continuous permafrost (Péwé, 1983). Both are within the northern limits of spruce (Little, 1971). As inferred from the mollusc and insect assemblages, climatic conditions indicated by the Elkader mammals are those associated with, but not entirely analogous to, modern subarctic parklands near the boreal forest/tundra transition zone.

WOODFORDIAN ENVIRONMENTS IN THE UPPER MISSISSIPPI VALLEY

Open-ground mammals, molluscs, and insects at Elkader outnumber forest dwellers both in numbers of species and individuals. Both mammals and insects from the basal units at Elkader indicate cold, near-tundra conditions in the area. Needles and twigs confirm that spruce was present, although it may have been stunted and restricted by slope exposure or insufficient moisture as suggested also by Morgan (1987) for ice-marginal communities. Distortion of sediments at Elkader suggests a periglacial origin for at least some units; this concurs with preserved ice-wedge casts, solifluction deposits, and other features in eastern Iowa, northern Illinois, and southwestern Wisconsin that are interpreted as being of similar origin (summarized in Péwé, 1983). Yet the sediments at Elkader also contain more temperate snail species that suggest the persistence of deciduous angiosperms at Elkader. If the various mollusc assemblages at Elkader and Elkader North are correctly interpreted as representing different, but temporally equivalent, microhabitats, then the uplands at the site were quite cold. However, hillsides and valley bottoms may have provided protection for some species of deciduous plants not normally associated with subarctic conditions. Collectively, the Elkader molluscs, insects, mammals, plant macrofossils, and stratigraphy indicate a subarctic environment dominated by open ground. This was similar to, but not entirely analogous with, modern subarctic parklands near the boreal forest/tundra ecotone.

Our interpretation of a cold full-glacial environment for northeastern Iowa at approximately 20,500 yr B.P. agrees with data from other Midwestern sites that indicate a transition to open vegetation about 22,700–21,400 yr B.P. (Baker et al., 1989a; Garry et al., 1990). Pollen and plant macrofossils from Wolf Creek, Morrison Co., Minnesota, reflect the existence of tundra-like vegetation between 20,500 and 14,700 yr B.P. (Birks, 1976). Likewise, insects at Saylorville, Iowa, (17,000 yr B.P. and 15,400–14,000

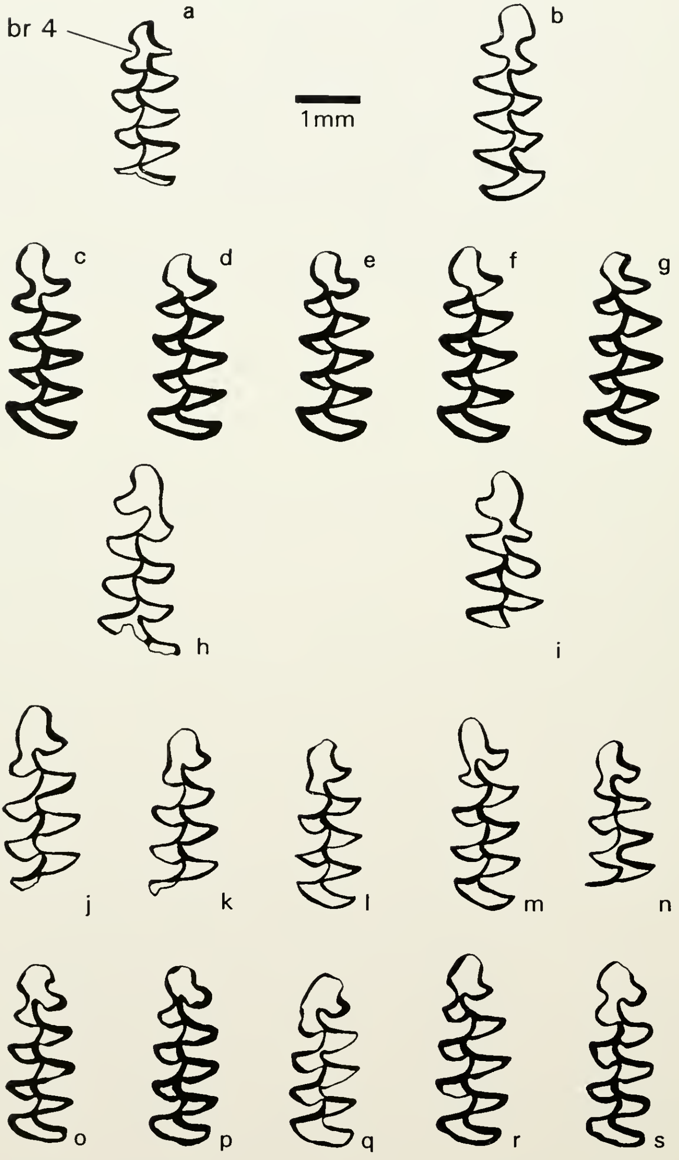


Fig. 8. Occusal patterns from lower, first molars of fossil *Microtus pennsylvanicus* from Elkader (a and b; SIU 49178), modern *M. pennsylvanicus alcorni* (c–g; KU 28878–80, 28882, 28884) from Alaska, fossil *Microtus* cf. *miurus* (h–n; SIU 49180) from Elkader, and modern *M. miurus muriei* (o–s; KU 51150–53, 51145) from Alaska. Occlusal patterns b, h, and i are from right molars; all others are from left molars. Abbreviation: br 4 = fourth buccal reentrant.

yr B.P.) are associated with tundra-like, open ground conditions (Schwert, 1992).

Conklin Quarry (Baker et al., 1986) is the one site geographically, temporally, and faunistically most comparable to Elkader. Both Conklin Quarry and Elkader indicate the presence of a cold environment with an abundance of open, tundra-like vegetation. The insect faunas and subsets of the molluscan faunas suggest that Conklin Quarry had a slightly more open vegetation, although comparisons of the molluscan assemblages from upland loess and the mammalian faunas indicate that Elkader may represent a colder environment. Differences between the two biotas reflect some combination of the difference in age of the two sites, varying proximity of the sites to Laurentide ice, individual responses of each species to climatic and physical variables, different microhabitats present at each site, and selective preservation of organisms. Nonetheless, Elkader and Conklin Quarry together indicate that subarctic conditions persisted in eastern Iowa between at least 20,500–17,200 yr B.P.

The nearly harmonious, low diversity arctic/subarctic mammalian assemblages of the full-glacial Elkader and Conklin Quarry sites contrast with the strongly disharmonious, diverse mammalian assemblage from Moscow Fissure (Foley, 1984). This site contains a nonanalogous assemblage of 21 mammal species dominated by boreal forms that include *Dicrostonyx torquatus, Clethrionomys* sp., and *Microtus xanthognathus,* but Moscow Fissure also contains western (e.g., *Thomomys talpoides,* western pocket gopher) and temperate, deciduous forest (e.g., *Blarina brevicauda,* short-tailed shrew) mammals. Foley (1984) interpreted the Moscow Fissure environment as a patchwork of marsh, steppe, and spruce parkland that was warmer than the full-glacial environments represented by the assemblages from Elkader or Conklin Quarry. The contrast between the assemblages from the two Iowa sites and Moscow Fissure apparently reflects the response of small mammals to regional climatic warming in the middle Woodfordian, a climatic change also detected by Baker et al. (1989a) in the younger (ca. 17,200–16,700 yr B.P.) portion of the pollen record from Conklin Quarry.

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